SPAWNING BIOMASS OF PACIFIC SARDINE (*Sardinops sagax*)
OFF CALIFORNIA IN 2003

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SUMMARY

The daily egg production of Pacific sardine (*Sardinops sagax*) off California from San Diego to Morro Bay was estimated to be 1.52/0.05m^2 (CV = 0.18) and the spawning biomass was estimated to be 485,121 mt (CV=0.36) for an area of 365,906 km^2, using the daily specific fecundity (number of eggs/population weight (gm)/day: 22.94 from the 2002 cruise (compared to 23.55 used in the years prior to 2002). The area is slightly larger than 325,082 km^2 estimated in 2002. The estimates of spawning biomass of Pacific sardine in 1994 and 1996 - 2003 are 127,000 mt, 83,000 mt, 410,000 mt, 314,000 mt, 282,000 mt, 1.06 million mt, 791,000 mt, 206,000 mt, and 485,000 mt respectively. Therefore, the estimates of spawning biomass have been fluctuated since 1994 .

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INTRODUCTION

The spawning biomass of Pacific sardine (*Sardinops sagax*) was estimated independently during 1986 (Scannel et al. 1996), 1987 (Wolf 1988a), 1988 (Wolf 1988b), 1994 (Lo et al. 1996), 1996 (Barnes et al. 1997), and 2002 (Lo and Macewicz 2002) using the daily egg production method (DEPM: Lasker 1985). DEPM estimates spawning biomass by: 1) calculating the daily egg production from ichthyoplankton survey data, 2) estimating the maturity and fecundity of females from adult fish samples, and 3) calculating the biomass of spawning adults. Before 1996, sardine egg production was estimated from direct CalVET plankton net sampling. Adult fish were sampled in various ways to obtain specimens for batch fecundity, spawning fraction, sex ratio, and average fish weight (Wolf, 1988a, 1988b, Scannell et al. 1996, Lo et al. 1996, Lo and Macewicz 2002).

Since 1996, in addition to CalVET and Bongo nets, the Continuous Underway Fish Egg Sampler (CUFES; Checkley, et al. 1997, Lo et al. 2001) has been used as a routine sampler for fish eggs, and data of sardine eggs collected with CUFES have been incorporated in various ways, depending on the survey design, in the estimation procedures of the daily egg production. In the1997 sardine egg survey (Hill et al. 1998), CUFES was used to allocate CalVET tows in an adaptive sampling plan. From 1998 to 2000, data of sardine eggs collected with both CalVET and CUFES during each April CalCOFI cruise were used to estimate daily egg production (Hill et al. 1999). Use of the full data sets from both samplers in the DEPM can be time consuming. Furthermore, the CUFES samples are exclusively from 3 m depth and it is not clear whether the distributions of sardine egg stages from CUFES samples are representative. Use of the CUFES data also requires an estimated conversion factor from eggs/min to eggs/$0.05m^2$. Starting with the 1999 April CalCOFI survey, an adaptive allocation survey design similar to the 1997 survey was implemented. In this design, CalVET tows are added in areas where they were not preassigned if sardine egg densities in CUFES collections are high.

Since 2001, a cost-effective alternative has been adopted to retain the DEPM index, but in a revised form that reduces effort in calculation and egg staging for CUFES collections. This revised DEPM index uses only CalVET samples of eggs and yolk-sac larvae in the high density area (Region 1) to provide an estimate of P_0, the variance of which can be large if sample size is fewer than 100 plankton tows.

In 2002, a full-scaled survey (San Diego to San Francisco) was conducted to estimate the spawning biomass of Pacific sardine. Adult sardine samples for reproductive output were taken aboard R/V *David Starr Jordan* after the routine CalCOFI cruise. In 2003, only ichthyoplankton samples were taken aboard R/V *Roger Revelle* and R/V *David Starr Jordan*.

MATERIALS AND METHODS

Data

Sardine eggs collected with both CalVET and CUFES during the April 2003 *Revelle* and *Jordan* cruises were the data sources for estimating the daily egg production of sardine. In addition to sardine eggs and yolk-sac larvae collected with the CalVET net, yolk-sac larvae collected with the Bongo net were included to model the sardine embryonic mortality curve since 2000. As in

2001 (Lo 2001), the CUFES data from the 2003 survey were used only to map the spatial distribution of the sardine spawning population. The survey area was later post-stratified into high density and low density areas according to the egg density from CUFES collections. Staged eggs from CalVET tows and yolk-sac larvae from CalVET and Bongo tows in the high density area were used to model embryonic mortality curve in the high density area and later converted to the daily egg production, P_0, for the whole survey area.

During the 2003 survey, the regular CalCOFI survey was extended to CaCOFI line 60.0 (north of Morro Bay) with the *Revelle* cruise (April 4 - 25) occupying six regular CalCOFI lines (93.0 - 76.6, 40 nm apart) and R/V *Jordan* occupying 10 lines (73.3- 60.0), half of which belonged to regular CalCOFI survey pattern (Figure 1). Bongo samples were taken on regular CalCOFI survey lines only. In addition, *Jordan* occupied six lines from line 95.0 north to line 75.0, 40 nm apart (Figure 2). Therefore, the total number of lines occupied by both vessels was 22 lines, 20 nm apart. For the *Jordan* cruise, CalVET tows were taken at 4 nm intervals on each line after the egg density from each of two consecutive CUFES samples exceeded 1 egg/min. Similarly, CalVET tows were stopped after the egg density from each of two consecutive CUFES samples was less than 1 egg/min. The threshold of 1 egg/min was reduced from the number used in years prior to 2002 (2 eggs/min) to increase the area identified as the high density area and, subsequently, to increase the number of CalVET samples. This adaptive allocation sampling, similar to the 1997 survey (Lo et al. 2001), was not used aboard *Revelle* because she was conducting routine CalCOFI sampling.

The survey area was post-stratified into two regions: Region 1, the high density area, and Region 2, the low density area. Region 1 encompassed the area where the egg density (eggs/min) in CUFES collections was at least 1 per minute. The rest of the survey area was Region 2 (Figure 1). One egg/min is equivalent to two to seven eggs/CalVET tow, depending on the degree of water mixing.

A total of 1287 CUFES samples was collected from both *Revelle* (437) and *Jordan* (850), at intervals ranging from 1 - 54 minutes with a mean of 24 minutes and median of 30 minutes. A total of 192 CalVET samples was collected, of which 127 contained at least one sardine egg (Table 1). Egg densities from each CalVET sample and from the CUFES samples taken within an hour before and after the CalVET tow, were paired and used to derive a conversion factor (E) from eggs/min of CUFES sample to CalVET catch. We used a regression estimator to compute the ratio of mean eggs/min from CUFES to mean eggs/tow from CalVET: $E = \mu_y / \mu_x$ where y is the eggs/min and x is eggs/tow.

Daily egg production (P_0)

Similar to the 2001 procedure (Lo 2001), we used the net tow as the sampling unit. Eggs from CalVET tows and yolk-sac larvae from both CalVET and Bongo tows in Region 1 were used to compute egg production based on data from 22 transects (lines 60-95) (Figure 1). A total of 116 of 133 CalVET samples in this region contained ≥ 1 sardine egg (Table 1); these eggs were examined for their developmental stages.

Based on aboard-ship counts of CUFES samples, among the 1287 collections, 514 were positive for sardines eggs. In Region 1, there were 347 positive CUFES collections out of 400 total collections. In Region 2, 167 of the total 887 collections were positive (Table 1).

For purpose of modeling the embryonic mortality curve, yolk-sac larvae are larvae ≤ 5 mm in reserved length. Yolk-sac larval production was computed as the number of yolk-sac larvae/$0.05m^2$ divided by the duration of the yolk-sac stage (number of larvae/$0.05m^2$/day), and the duration was computed based on the temperature-dependent growth curve (Table 3 of Zweifel and Lasker 1976) for each tow. For yolk-sac larvae caught by the Bongo net, the larval abundance was further adjusted for size-specific extrusion from 0.505 mm mesh (Table 7 of Lo 1983), and for the percent of each sample that was sorted. The adjusted yolk-sac larvae/0.05 m^2 was then computed for each tow and was termed daily larval production/0.05 m^2.

In the entire survey area, 53 of 192 CalVET and 29 of 94 Bongo samples had at least one yolk-sac larva. In Region 1, 38 of 125 CalVET, and 11 of 15 Bongo samples were positive for yolk-sac larvae. In region 2, 15 of 67 CalVET and 18 of 79 Bongo samples were positive for yolk-sac larvae (Table 1, Figure 2).

Daily egg production in Region 1 ($P_{0,1}$)

Sardine eggs and yolk-sac larvae and their ages were used to construct the embryonic mortality curve (Lo et al. 1996, Lo 2001). Sardine egg density for each developmental stage was computed based on CalVET samples (Figure 3). The density of eggs in 2003 was much higher than it was in 2002 and similar to 2001. The density of stage 6 was highest among all stages. A temperature-dependent stage-to-age model (Lo et. al. 1996) was used to assign age to each stage. Sardine eggs and estimated ages were used directly in nonlinear regression. The 3-h old eggs and eggs older than 2.5 day were excluded because of possible bias. The average temperature for CalVET tows with ≥ 1 egg was 13.8° C, similar to the 13.6° C average in 2002.

The sardine embryonic mortality curve was modeled by an exponential decay curve (Lo et al. 1996):

$$P_t = P_0 \exp(-zt)$$ [1]

where P_t is either eggs/$0.05m^2$/day from CalVET tows or yolk-sac-larvae/$0.05m^2$/day from CalVET and Bongo tows, and t is the age (days) of eggs or yolk-sac larvae from each tow. A weighted nonlinear regression was used to estimate two parameters in equation (1) where the weights are 1/SD. SDs of eggs were 8.395,12.334, and 5.85, for day one, day two and day three age groups respectively. The SD of yolk-sac larval production from CalVET was 0.513 and the SD of yolk-sac larval production from Bongo samples was 1.185. All the standard deviations were higher than those in 2002 (Lo and Macewicz, 2002), mostly likely due to the higher densities of eggs and larvae.

A simulation study (Lo, 2001) indicated that $P_{0,1}$ computed from a weighted nonlinear regression based on the original data points has a relative bias (RB) of -0.04 of the estimate where the RB= (mean of 1000 estimates - true value)/mean of 1000 estimates. Therefore the bias-corrected estimate of $P_{0,1,c} = P_{0,1} * (1- RB) = P_{0,1} *(1.04)$, and SE $(P_{0,1,c}) = $ SE$(P_{0,1}) * 1.04$.

Daily egg production in Region 2 ($P_{0,2}$)

Although 59 CalVET samples were taken in Region 2, only 11 tows had sardine eggs ≥ 1, ranging from 1 to 15 eggs per tow. Therefore, we estimated daily egg production ($P_{0,2}$) as the product of the egg production in Region 1 ($P_{0,1,c}$) and the ratio of egg density in Region 2 to Region 1 (q) from CUFES samples, assuming the catch ratio of eggs/min from CUFES to eggs/tow from CalVET is the same for the whole survey area:

$$P_{0,2}=P_{0,1,c}\ q \qquad [2]$$

$$q=\frac{\sum_i \frac{\overline{x}_{2,i}}{\overline{x}_{1,i}}\ m_i}{\sum_i m_i} \qquad [3]$$

$$var(q)=\frac{[n/(n-1)]\sum_i m_i^2(q_i-q)^2}{(\sum_i m_i)^2}$$

where q is the ratio of eggs/min between low density area and high density areas, m_i was the total CUFES time (minutes) in the ith transect, $\overline{x}_{j,i}$ is eggs/min of the ith transect in the jth Region, and $q_i=\frac{\overline{x}_{2,i}}{\overline{x}_{1,i}}$ is the catch ratio in the ith transect.

Daily egg production for the whole survey area (P_0)

P_0 was computed as a weighted average of $P_{0,1}$ and $P_{0,2}$:

$$\begin{aligned}P_0&=\frac{P_{0,1,c}A_1+P_{0,2}\ A_2}{A_1+A_2}\\&=P_{0,1,c}w_1+P_{0,2}\ w_2\\&=P_{0,1,c}[w_1+q\ w_2]\end{aligned} \qquad [4]$$

and

$$mse(P_0)$$
$$= mse(P_{0,1,c})(w_1+w_2q)^2 + P_{0,1,c}^2 w_2^2 V(q) - mse(P_{0,1,c})w_2^2 V(q)$$

(Goodman, 1960) where $mse(p_{0,1,c}) = v(p_{0,1}) + (p_{0,1} RB)^2$

and $w_i = \dfrac{A_i}{A_1+A_2}$, and A_i is the area size for $i = 1, 2$.

Spawning biomass (B_s)

The spawning biomass was computed according to:

$$B_s = \frac{P_0\ A\ C}{R\ S\ F/W_f} \qquad [5]$$

where A is the survey area in unit of 0.05 m^2, S is the proportion of mature females that spawned per day, F is the batch fecundity (number of eggs per mature female), R is the fraction of mature female fish by weight (sex ratio), W_f is the average weight of mature females (gm), and C is the conversion factor from gm to mt. P_0A is the total daily egg production in the survey area, and the denominator (RSF/W_f) is the daily specific fecundity (number of eggs/population weight (gm)/day), which was estimated from 2002 survey data (Lo and Macewicz, 2002): 22.94 eggs/gm/day.

The variance of the spawning biomass estimate $\left(\hat{B_s}\right)$ was computed from the Taylor expansion and was expressed in terms of the coefficient of variation (CV) for each parameter estimate and covariance for adult parameter estimates (Parker 1985):

$$VAR\left(\hat{B}_s\right) = \hat{B}_s{}^2 \left[CV\left(\hat{P}_0\right)^2 + CV\left(\hat{W}_f\right)^2 + CV\left(\hat{S}\right)^2 + CV\left(\hat{R}\right)^2 + CV\left(\hat{F}\right)^2 + 2COVS \right] \qquad (6)$$

The covariance term on the right-hand side is

$$COVS = \sum_i \sum_{i<j} sign \frac{COV(x_i, x_j)}{x_i x_j}$$

where x's are the adult parameter estimates, and subscripts i and j represent different adult parameters; e.g., $x_i = F$ and $x_j = W_f$. The sign of any two terms is positive if they are both in the numerator of B_s or denominator of B_s (equation 5); otherwise, the sign is negative. Only $CV(p_0)$ was estimated from 2003 data whereas other CV's were from 2002 trawl survey data: Equation (6) can be expressed as

$$VAR\left(\hat{B}_s\right) = \hat{B}_s^{\,2}\left[CV\left(\hat{P}_0\right)^2 + allCVsCOVS\right]$$

where

$$allCVsCOVs = \left[CV\left(\hat{W}_f\right)^2 + CV\left(\hat{S}\right)^2 + CV\left(\hat{R}\right)^2 + CV\left(\hat{F}\right)^2 + 2COVS\right]$$

From 2002 trawl survey data, we obtained estimate of $allCVsCOV = 0.0944$.

RESULTS

Daily egg production (P_0)

The daily egg production in Region 1 ($P_{0,1}$) was 5.82/0.05m^2/day (CV=0.18) and egg mortality was Z=0.48 (CV=0.08) for an area of 82,578km^2 (24,128 nm^2) (equation 1 and figure 4). The bias-corrected egg production, ($P_{0,1,c}$) is 6.05 (CV=0.18) (Table 2). The ratio (q) of egg density between Region 2 and Region 1 from CUFES samples was 0.033 (CV=0.025) (equation 3). In Region 2, the egg production ($P_{0,2}$) was 0.2 /0.05 m^2/day (CV=0.322) for an area of 283,328 km^2 (82,784 nm^2). The estimate of the daily egg production for the entire survey area was 1.52/0.05 m^2 (CV=0.18) (equation 4) for a total area of 365,906 km^2 (106,912 nm^2) (Table 2). Egg mortality, Z, was 0.48(CV=0.08), similar to 2002 0.4(CV=0.15). Z values for other years are: 2001: 0.37 (CV=0.21), 2000: 0.42 (CV=0.73), 1999: 0.1 (CV=0.6) and 1998: 0.255 (CV=0.37) (Table 3).

Spawning biomass (B_s)

The final estimate of spawning biomass of sardine in 2003 (equation 5) was 485,121 mt (CV=0.36) (x 1.1 = 533,633 short ton) for an area of 365,906 km^2 (106,912 nm^2) from San Diego to Morro Bay. The point estimates of spawning biomass of Pacific sardine in 1994 and 1996 - 2002 are 127,102; 83,176; 409,579; 313,986; 282,248; 1,063,837; 790,925 and 206,333 mt (Table 3). If we assume the daily specific fecundity in 2003 was the same as 1986-1994 (23.55 eggs/gm of population), sardine spawning biomass in 2003 would be 472,380 mt which most likely is not significantly different from the final estimate of 485,121 mt (Table 2).

Catch ratio between CUFES and CalVET (E)

Although this ratio is no longer needed in the current estimation procedure, we computed it for comparison purposes. The catch ratio of eggs/min to eggs/tows (eggs/min $= E *$ eggs/0.05 m^2) was computed from 122 pairs of eggs/0.05 m^2 from CalVET tows and eggs/min from CUFES collections. The eggs/min corresponding to each positive CalVET tow was the mean eggs/min from all CUFES collections taken from one hour before to one hour after each positive CalVET Tow (Figure 5). The catch ratio was 0.39 (CV=0.11). A ratio of 0.39 means that one egg/tow from

CalVET tow was equivalent to approximately 0.39 egg/min from a CUFES sample, or one egg/minute from the CUFES was equivalent to 2.56 eggs/tow from the CalVET sample.

DISCUSSION

Computation of P_0

The embryonic mortality curve is primarily based on number of eggs colleted from CalVET and yolk-sac larvae at developmental stages collected from CalVET and Bongo. The distribution of density of eggs by stage (Figure 3) indicated that density of eggs of stage 6 was the highest among all stages. This phenomena was also observed in many previous sardine egg surveys (Bentley et al. 1995, Lo 2001, Lo et al 2001, and Lo and Macewicz 2002). This may be resulted from possible long duration of stage-6 eggs, degree of patchiness or both. Further investigation is warranted to ascertain the distribution of stages and to understand the underlying reasons.

As mentioned in the 2002 report, since 2001, the weighted nonlinear estimator based on original data has been used with a correction for the bias. Other possible improvements of our estimation procedure would be to use weighted averages of estimates from past years, e.g., mortality rate and the ratio of eggs/min in the low density area to the high density area, *q*. The weights would be the inverse of the variance of the estimate in each of the past years, assuming there is no trend through time (Pena 1997). A Bayesian estimation procedure has been developed where the estimate of P_0 is a weighted average of the estimate from the current year and Bayesian estimates based on data of past years. The Bayesian estimation procedure needs to be evaluated by a simulation study before its implementation to our spawning biomass estimation procedure.

Catch ratio between CUFES and CalVET (E)

The 2003 catch ratio between CUFES and CalVET (0.39) was slightly higher than those obtained in the past years: 1998 (0.32), 1999 (0.34), 2000 (0.277), and 2001 (0.145(CV=0.026)) 2002 (0.24(CV=0.06)). This value of 0.39 was again quite different from the 1996 estimate of 0.73. This could be because the 1996 CalVET samples were taken only in the southern area near San Diego while since 1997, CalVET samples were taken in a larger area north of San Diego.

Spawning biomass

The estimate of spawning biomass is considerably higher than that in 2002 but lower than 2001. These differences are primarily due to the change of the egg production, 1.52 eggs/0.05m^2, compared to 2.9 eggs/0.05m^2 in 2001 and 0.728 eggs/0.05m^2 in 2002, while the area of region 1 (22.5% of the total survey area) in 2003 was similar to 2001 (21%) and smaller than 2002 (27%). The daily specific fecundity of 22.94 eggs/gm/day in 2002 was used for the 2003 estimate of spawning biomass since no trawl samples were taken in 2003.

ACKNOWLEDGMENTS

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Table 1. Number of positive tows of sardine eggs from CalVET, yolk-sac larvae from CalVET and Bongo, and eggs from CUFES in Region 1 (eggs/min ≥1) and Region 2 (eggs/min <1) for both *Revelle* (RR) and *Jordan* (Jord) cruises 0304.

		Region						Total	RR	Jord
		1			2					
		Total	RR	Jord	Total	RR	Jord			
CalVET eggs	positive	116	5	111	11	5	6	127	10	117
	Total	133	7	126	59	35	24	192	42	150
CalVET yolk-sac	positive	38	6	32	15	6	9	53	12	41
	Total	125	6	119	67	36	31	192	42	150
Bongo yolk-sac	positive	11	5	6	18	17	1	29	22	7
	Total	15	6	9	79	60	19	94	66	28
CUFES eggs	positive	347	47	300	167	51	116	514	98	416
	Total	400	55	345	887	382	505	1,287	437	850

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Table 2. Estimates of egg production (P_o) of Pacific sardine in 2003 based on egg data from Calvet and yolk-sac larval data from CalVET and Bongo in region 1 (eggs/min $\geq$1) and region 2 (eggs/min<1) from both Revelle and Jordan (April 4-30) cruises and the spawning biomass of sardine in 2003. Estimates of adult parameters were from 2002 and 1994 cruises.

Parameter		region 1	region 2	Whole area	
n: pump (excluding the home-bound track)		400	887	1287	1287
n: Calvet		133	59	192	192
p0/0.05m^2	Calvet	6.053[1]	0.20	1.52	1.52
CV		0.179	0.322	0.18	0.18
Area		82578	283328	365906	365906
km^2;%		22.57	77.43	100	100
Year for data collection of adult parameters				1994	2002
Fish wt(W)				82.5	159.25
Batch fecundity(F)				24283	54403
Spawning freq(S)				0.149[2]	0.1739
Sex ratio(R)				0.537	0.386
Eggs/gm biomass(RSF/W)				23.55	22.931
S. biomass(mt)				472380	485121
CV					0.36
Daily mortality(Z)		0.48			
CV		0.08			
eggs/min		6.5	0.13	1.57	
CV		0.29	0.48	0.27	
q=eggs/min in reg 2 / eggs/min in reg 1				0.033	
CV				0.025	
E=eggs.min/eggs/tow				0.39	
CV				0.11	
n: bongo		15	79	94	
Area in nm^2		24128	82784	106912	106912
S. biomass(ston)				519617	533633

p0/0.05m2 was from Calvet only for 2001 and beyond
[1]6.053 was bias-corrected for 5.82, estimate of p_0, from weighted regression.
[2]0.149 was computed based on data collected during 1986-1994 (Table 8 of Macewicz et al. 1996)

Table 3. Estimates of daily egg production (P_0) for the survey area from San Diego to Monterey, daily instantaneous mortality rates (Z) from high density area and spawning biomass of Pacific sardine for 1994, 1996 - 2003.

Year	P_0 [a](CV)	Z (CV)	Area(km^2)	Spawning biomass (mt)[b](CV)	Ave. Temperature for CalVET samples with eggs>0 (C^o)	Methods for P_0
1994	0.193(0.21)	0.12(0.91)	380,175	127,102	--	Weighted nonlinear on grouped data
1996	0.415(0.42)	0.105(4.15)	235,960	83,176	14.5	Composite estimate
1997	2.77(0.21)	0.35(0.14)	174,096	409,579	13.7	Weighted nonlinear on grouped data
1998	2.279(0.34)	0.255(0.37)	162,253	313,986	14.38	Composite estimate
1999	1.092(0.35)	0.10(0.6)	304,191	282,248	12.5	Composite estimate
2000	4.235(0.4)	0.42(0.73)	295,759	1,063,837	14.1	Composite estimate
2001	2.898(0.39)	0.37(0.21)	321,386	790,925	13.3	Weighted nonlinear on original data
2002	0.728(0.17)	0.4(0.15)	325,082	206,333 (0.35)	13.6	Weighted nonlinear on original data
2003	1.52(0.18)	0.48(0.08)	365,906	485,121 (0.36)	13.8	Weighted nonlinear on original data

[a] Zs were computed from weighted linear regression on the original data except for 1994 and 1997.
[b] The spawning biomass of 1994 was based on 11.38 eggs per gram of population weight. For 1996-2001, the spawning biomass was based on 23.55 eggs per gram of population weight.

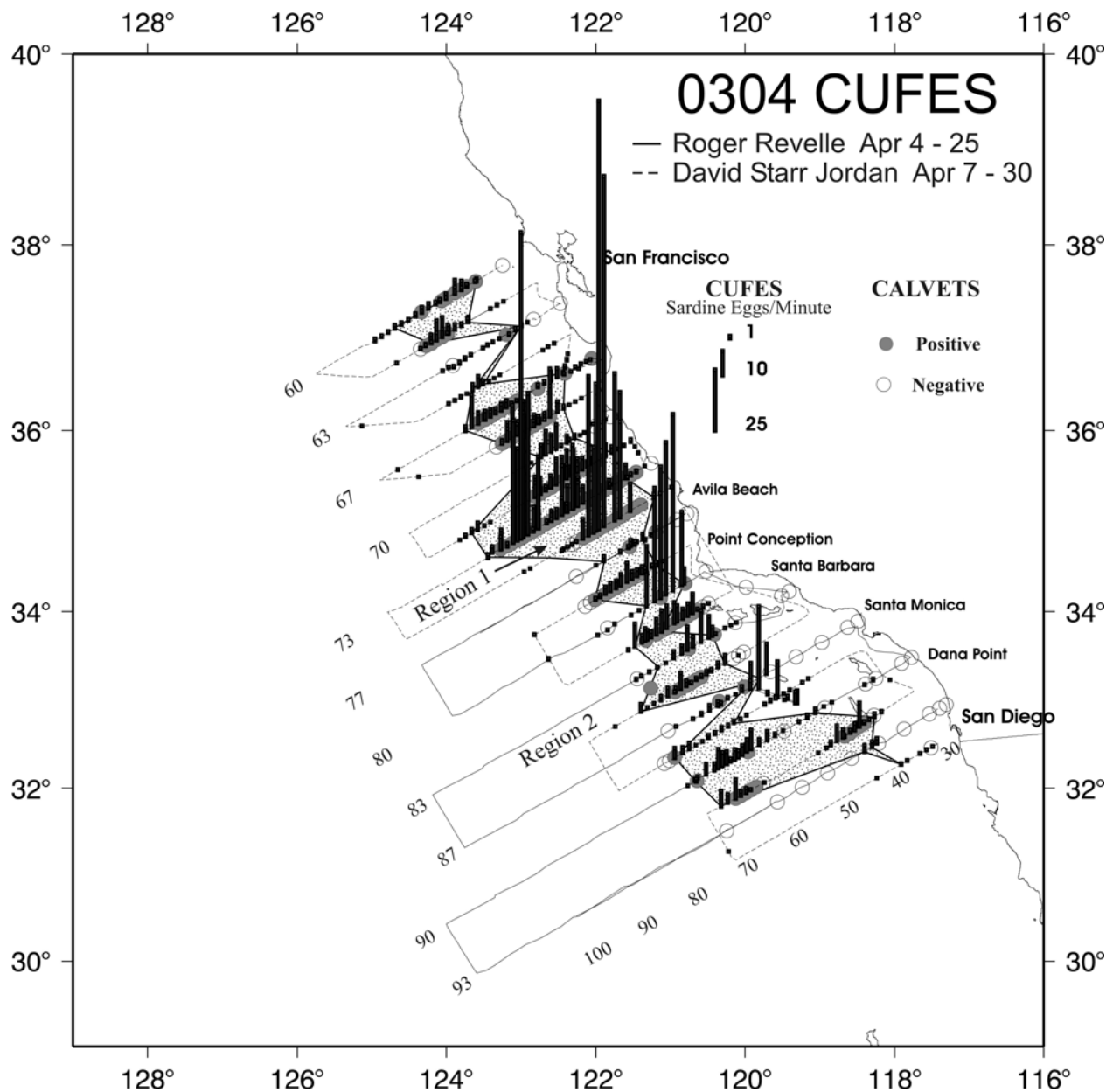*This page intentionally left blank.*

Figure 1. Sardine eggs from CalVET (or Pairovet; solid circle denotes positive catch and open circle denotes zero catch) and from CUFES (stick denotes positive collection) in April 2003 survey. The numbers on line 93 are CalCOFI station numbers. Region 1 is stippled area.
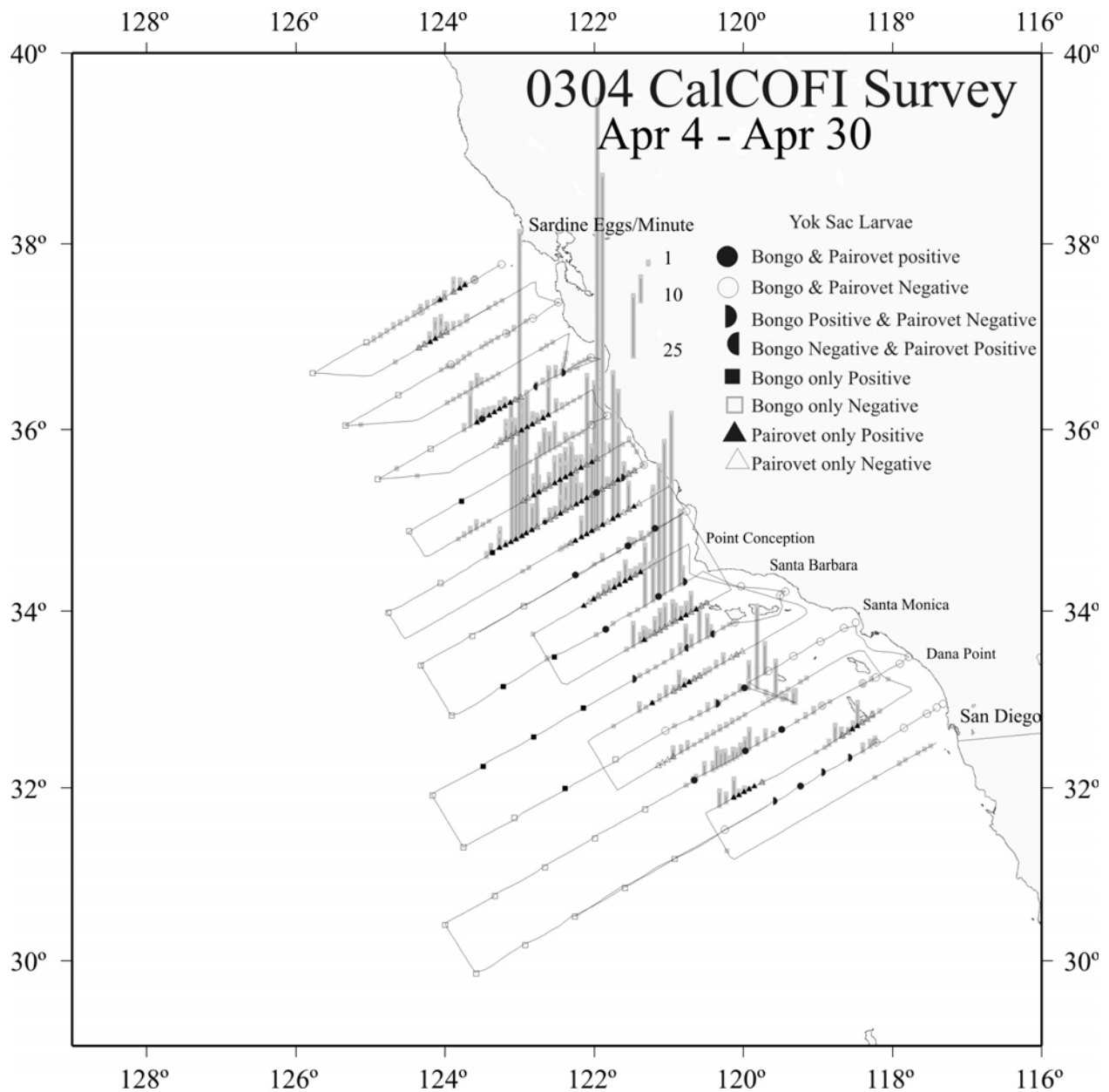
Figure 2. Sardine yolk-sac larvae from CalVET (or Pairovet; circle and triangle) and from Bongo (circle and square) in April 2003 survey. Solid symbols are positive and open symbols are zero catch.
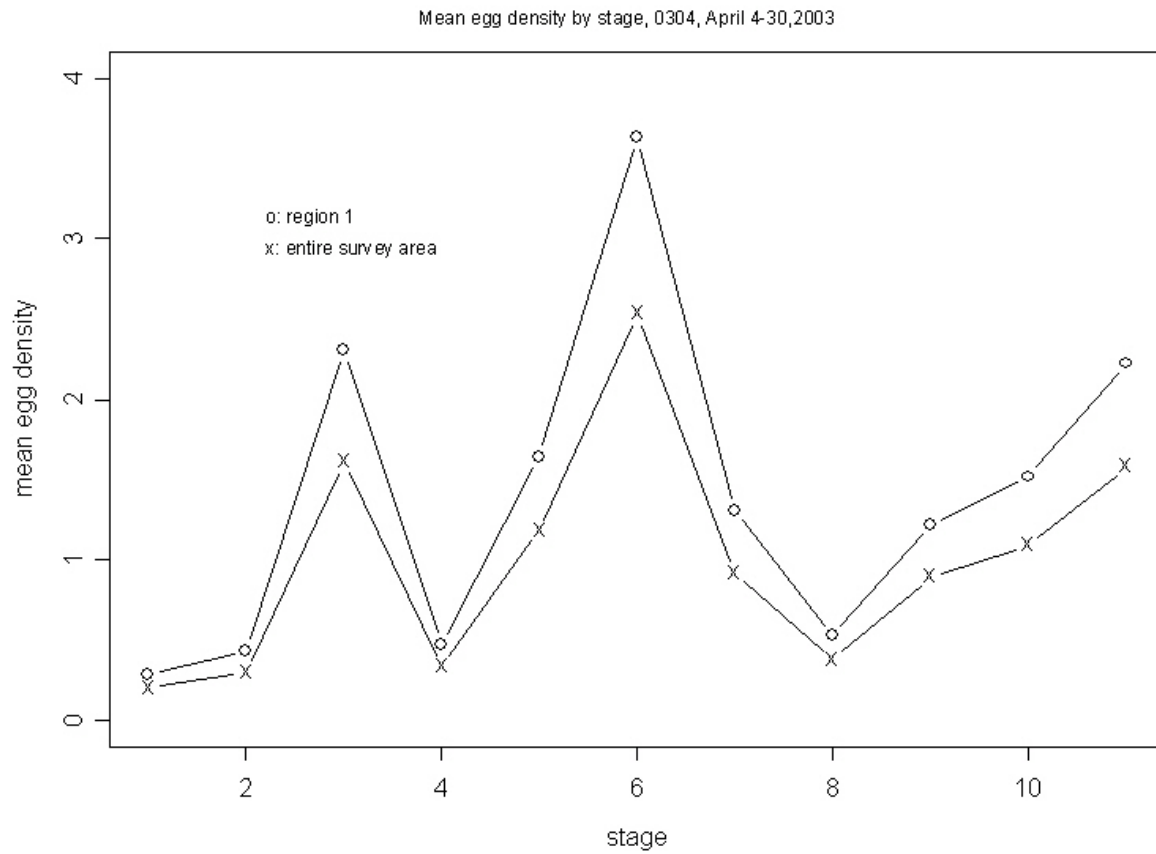
Mean egg density by stage, 0304, April 4-30, 2003

o: region 1
x: entire survey area

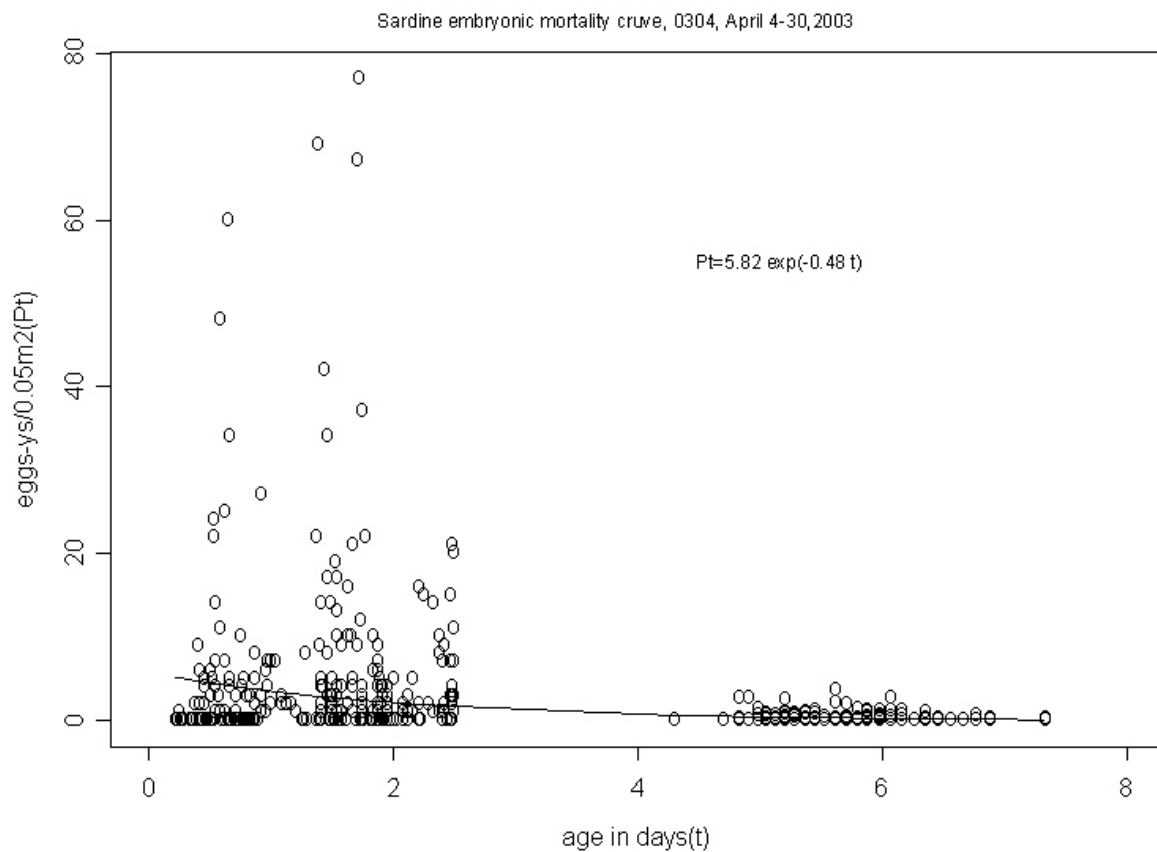**Figure 3.** Sardine eggs per 0.05m^2 for each developmental stage.

Figure 4. Embryonic mortality curve of Pacific sardine of 2003. Staged egg data were from CalVET and yolk-sac larval data were from CalVET and Bongo. The number, 5.82, is the estimate of daily egg production, before corrected for bias.
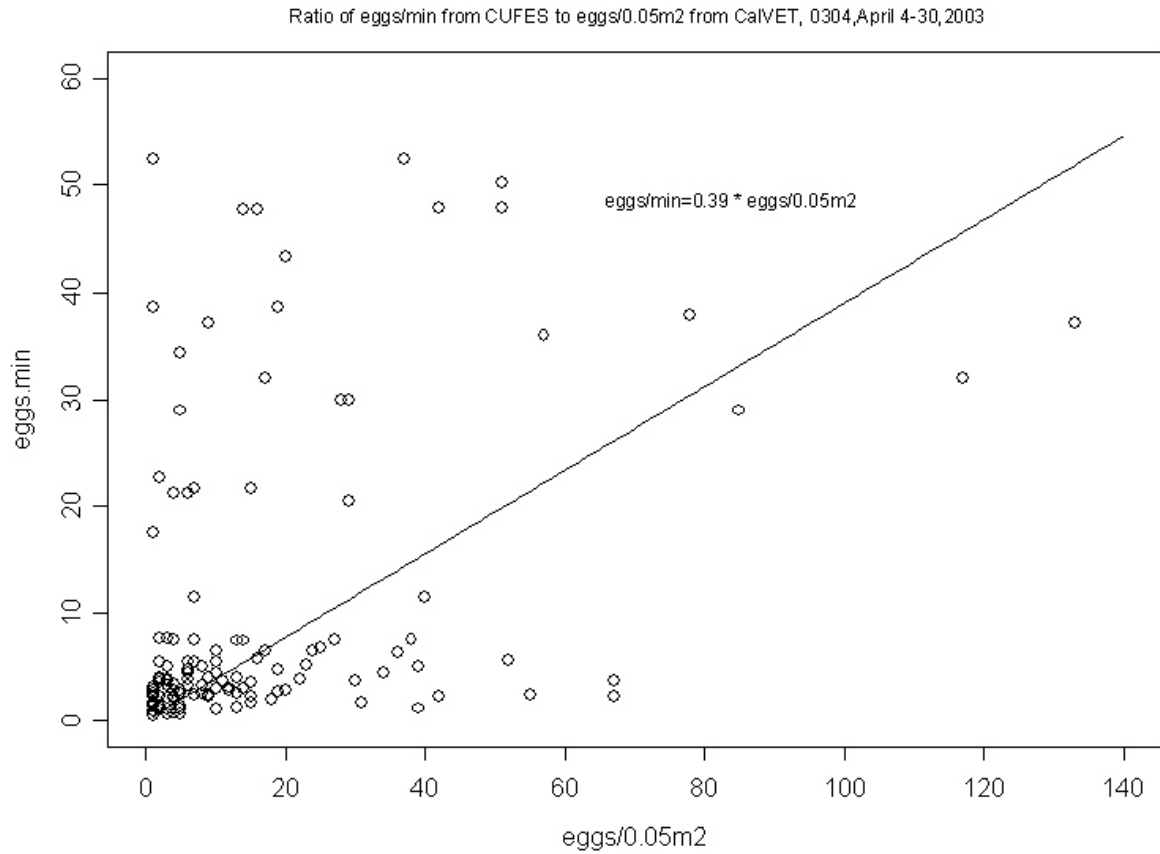
Figure 5. Catch ratio of eggs/min from CUFES to eggs/0.05m^2 from CalVET during April 2003.